

# A HISTORICAL SKETCH OF THE VEGETATION OF THE MOJAVE AND COLORADO DESERTS OF THE AMERICAN SOUTHWEST<sup>1</sup>

ROBERT F. THORNE<sup>2</sup>

## ABSTRACT

The Mojave and Colorado Deserts of the American Southwest are geologically recent in origin, resulting primarily from the rain-shadow caused by the Late Pliocene-Pleistocene elevation of the Sierra Nevada, Transverse, and Peninsular ranges. Their age thus is perhaps two to three million years. The present vegetation is even more recent, largely Holocene in origin, and still evolving. During the last, Wisconsin, glacial episode the California deserts were well supplied with huge, deep lakes and large streams and an open woodland, possibly grassy, supporting numerous large mammals, now mostly extinct. The desert flora, however, is in large part more ancient, having been assembled since early Paleogene time from many sources. Most of the perennials are probably former members of the Madro-Tertiary Geoflora that dominated southern California and adjacent areas during the Tertiary. They are species of dry habitats preadapted to long periods of drought, hot, dry summers, and cool, wet winters and thus able to populate and adapt to the varied desert habitats when they became available. They survived cool, pluvial, glacial periods by migration southward or to lower elevations. Some elements of the American southwestern desert flora are derived from Mexico, South America, central Asia, and a few possibly from North Africa and the Mediterranean region by overland immigration or long distance dispersal. In some instances this was aided by changing ocean size due to continental movement, glacial sea-level lowering, and to changes in oceanic-current patterns. Some desert plants, at least some of the ephemerals, may well be of very recent, even Holocene, origin in our arid Southwest.

Those of us without much geological training, in view of our own brief life span, tend to think of large-scale features of the landscape as rather permanent, thus very ancient. Yet geologists assure us that large lakes, islands, mountains, and the deserts behind them are relatively ephemeral in the geological time scale. Our southwestern deserts are no exception. The existing regional deserts or semi-deserts are geologically recent, possibly only a couple of million years old, at least as we know them today. They are essentially products of the late Pliocene-Pleistocene elevation of the Sierra Nevada, Transverse, and Peninsular ranges in southern California, which created a huge rain-shadow to the east. Thus, most of the moisture gleaned from the Pacific Ocean by the prevailing westerly winds precipitated on the western slopes of the ranges. As the air masses descended the transmontane slopes, they heated up adiabatically and became a drying force.

## REGIONAL GEOLOGY

It is impossible to obtain exact dating for incidents of regional uplift. Often we must rely

heavily upon circumstantial evidence presented by juxtaposition of strata, by radiometric dating of volcanic rocks, or by fossil floras and faunas of the region. When properly dated, fossil assemblages of plants and animals allow us to infer much about the past vegetation and climatic conditions of periods in question and the changes that have taken place. Leaves that are mostly large, entire-margined, and evergreen indicate warm-temperate to tropical forest conditions, and large numbers of grazing mammals presumably require rather extensive savannas or open grasslands.

Oakeshott (1971) reported that radiometric dating of volcanic rocks indicated "that the intensive faulting of the eastern side of the Sierra (accompanied by uplift and westward tilting) began about 2.5 million years ago." Paleoclimatic evidence from fossil floras of the region indicates that until that time the Sierra Nevada was a range with only low to moderate relief and that it became a major topographic barrier after the close of the Pliocene (Axelrod, 1962; Axelrod & Ting, 1960). From reconstructed stream profiles and paleobotanical evidence Axelrod estimated total

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<sup>2</sup> Rancho Santa Ana Botanic Garden, Claremont, California 91711.



post-Pliocene uplift in the Yosemite region at 1,980–2,135 m. Likewise he placed total post-Pliocene displacement at Donner Summit at about 1,525 m, at Carson Pass at about 2,135 m, and at Mount Whitney at about 2,745 m (Axelrod, 1962). Bachman (1978) estimated that “Relative uplift between Owens Valley and the White-Inyo Mountains may have been as much as 2,300 m during the past 2.3 m.y.”

According to Foster (1980) the central Transverse Ranges during the late Cenozoic Era evolved from an area of low relief to a region of rugged high mountains. He estimated that the “Uplift of the San Gabriel Mountains began at least in Crowder time, 4–2 m.y.b.p., and possibly earlier. Erosion followed and uplift renewed as the upward coarsening Harold and Shoemaker deposits formed in Rancholabrean time, approximately 600,000–100,000? yr.b.p.” He also believed that the San Bernardino Mountains had only moderate relief in late Hemphillian-Blancan time [Late Miocene, 5–8 Ma], but were worn down to a pediment (an area of low relief) by Crowder time (Plio-Pleistocene). The elevation of the San Bernardino Mts. by Upper Pleistocene time is attested to by the glacial deposits on San Geronio Peak.

Because folded and faulted strata of Lower Pleistocene time in the Ventura Basin portion of the western Transverse Ranges are overlain unconformably by upper Pleistocene beds, Oakeshott (1971) concluded that “one of the most violent mountain-building pulses was clearly in the middle Pleistocene.” In reference to the San Gabriel Mountains, Oakeshott described the great mid-Pleistocene orogeny as “very widespread, involving uplift, tight folding, major faulting, and general destruction of the Tertiary basins by mountain-building processes . . . . Crustal movements have continued to the present day.” Bull (1978) estimated that uplift rates along the south side of the San Gabriel Mountains appear to average about 1 to 3 m per 1,000 years. Indeed the youthful ruggedness of the range and the all too-frequent earthquakes in the area attest to the continued mountain building.

The fossil Soboba Flora (Axelrod, 1980a) west of the San Jacinto Mountains of southern California is now dated at about 1.75 Ma in Early Pleistocene time. From the plant species and plant communities represented in the fossil flora, Axelrod (1966) believed that the nearby San Jacinto Peak then stood at about 2,135 m compared to its 3,302 m today. Axelrod estimated that the

major Transverse and Peninsular ranges then had elevations about half those of the present day. It would appear that the San Jacinto Mountains, at least, gained nearly 1,220 m in elevation since the Early Pleistocene.

In the Colorado Desert (i.e., the Lower Colorado River Valley subdivision of the Sonoran Desert) of extreme southern California the Salton Basin shows convincing evidence, according to Oakeshott (1971), of “great vertical displacements in late geologic history . . . displacement within the Salton Trough is going on very rapidly.” Lindsay and Lindsay (1978), discussing the Pleistocene vertical faulting of the Peninsular Range ridges on the western side of the Salton Trough, believed that the “resulting ‘rain-shadow’ effect, coupled with drying of California climates in general, caused an arid climate to develop here, and a desert evolved about 20,000 years ago.” Admitting the problematic accuracy of some of these dates, one must still conclude that the California regional deserts are indeed geologically a very recent phenomenon.

During Late Wisconsin and Holocene Transition time, under a cool, moist, pluvial climate, the California deserts were supplied with an extensive river and lake system. It is estimated that as much as 20 percent of the Mojave Desert was covered by fresh water to an average depth of 30 m (G. Jefferson, pers. comm.). Searles Lake, for example, was estimated at 132 m deep and 26 km long, Lake Panamint at 280 m deep and 100 km long, Lake Manly of Death Valley at 275 m deep and 175–240 km long, and Lake Manix at 60 m deep and 515–775 sq km in area (Blanc & Cleveland, 1961; Oakeshott, 1971). Until it disappeared about 500 years ago, Lake Cahuilla, a predecessor of the Salton Sea, filled the Salton Basin with about 5,180 sq km of fresh water (Lindsay & Lindsay, 1978).

#### TERTIARY VEGETATION IN SOUTHERN CALIFORNIA

It may be of some interest to examine the past vegetation of our present deserts and adjacent regions of southern California. Presently, according to my moderately liberal classification, there are 140 angiosperm families indigenous in California. The state had a much richer family representation in the Tertiary. Both mega- and microfossils indicate that at least 40 more angiosperm families were present in California during Late Cretaceous and Tertiary time (not to



mention at least nine additional families of pteridophytes and gymnosperms) (Potbury, 1935; MacGinitie, 1937, 1941; Axelrod, 1950e, 1958, 1973; Drugg, 1967; Jarzen, 1980; Page, 1981) but have been eliminated from the flora by changed climatic conditions. Presumably other, especially herbaceous, families failed to be fossilized or to be recognized. Many of these now exotic families are found today to the south in Baja California or east in southern Arizona, often near California's borders, such as the Malpighiaceae, Menispermaceae, Moroideae, Passifloraceae, Sapindaceae, and Sapotaceae. Others can be found in the Cape Region of Baja California, subtropical Sonora or Sinaloa, or farther south in Mexico, as Aquifoliaceae, Bombacaceae, Buxaceae, Chloranthaceae, Chrysobalanaceae, Clethraceae, Combretaceae, Dilleniaceae, Ebenaceae, Flacourtiaceae, Gunneraceae, Hamamelidaceae, Icacinaceae, Illiciaceae, Magnoliaceae, Meliaceae, Myrtaceae, Nelumbonaceae, Nyssaceae, Proteaceae, Sabiaceae, Symplocaceae, Theaceae, and Tiliaceae. Others today find refuge in eastern Asia, as Alangiaceae, Cercidiphyllaceae, and Trapaceae, or in Australia, as Alangiaceae and Eupomatiaceae.

#### PALEOGENE

Early in the Tertiary the topography and climate of California was very different from the present, and tropical seas covered much of coastal and central California. Much of southern California west of the San Andreas fault had not yet joined the state, being then part of Baja California, which in turn was part of mainland Mexico, the Gulf of California not yet having been formed. Topography was low and rolling, and temperate (cloud) to subtropical rainforest apparently covered the coast, and subtropical savanna and dry tropical (short-tree) forest probably covered much of the interior, possibly with oak woodland on the highlands above. Farther north a lush evergreen-deciduous hardwood forest similar to that found today in southeastern China, vegetated much of the state's interior (Potbury, 1935; MacGinitie, 1937, 1941; Axelrod, 1950e, 1958, 1973, 1979; Raven & Axelrod, 1977).

#### MIOCENE

During the long Miocene Epoch the region that presently forms southern California supported in coastal areas and on moister slopes inland a generalized woodland of sclerophyllous trees dom-

inated by live oaks (*Quercus*) and laurels (*Persea*, *Ocotea*, *Nectandra*, and *Umbellularia*), but with a rich assemblage of other genera as well, including *Acer*, *Annona*, *Bumelia*, *Cedrela*, *Clethra*, *Dioon*, *Ficus*, *Ilex*, *Juglans*, *Laurocerasus*, *Lithocarpus*, *Lyonothamnus*, *Magnolia*, *Myrica*, *Pinus*, *Platanus*, *Populus*, *Prunus*, *Sabal*, and *Sapindus*, as found variously in the Anaverde, Mint Canyon, Mount Eden, Puente, Piru Gorge, and Temblor floras (Axelrod, 1937, 1939, 1940, 1950b, 1950c, 1950d, 1973). This vegetation thrived on ample summer rainfall and a mild climate with no frost in winter. As Miocene climate became drier and cooler, many of the genera were forced south out of mainland California. Those genera left in Alta California are found now scattered in island oak woodland, riparian woodlands, southern mixed evergreen forest, or other more mesic communities. Closed-cone conifer forests (dominated by pines equivalent to modern *Pinus muricata* D. Don and *P. radiata* D. Don) occupied sheltered slopes by the ocean (Axelrod, 1980b).

In the drier interior, particularly in the present desert regions, oak woodland covered the lowlands with riparian woodland following the waterways. Characteristic of the woodland-savannas were *Quercus*, *Pinus*, *Cupressus*, *Aesculus*, *Juglans*, and *Robinia* and of the riparian woodlands *Acer*, *Brahea*, *Bumelia*, *Celtis*, *Juglans*, *Lyonothamnus*, *Platanus*, *Populus*, *Sabal*, *Salix*, and *Sapindus*. Chaparral occupied the well-drained slopes, short-tree forest the moister slopes, and subtropical thornscrub the rocky, lower, drier slopes. All of these communities, like the coastal sagescrub (Axelrod, 1978), closed-cone conifer forest (Axelrod, 1980b), and oak-laurel woodland, belong to the Madro-Tertiary flora, which had apparently evolved on dry sites during the Eocene out of the warm-temperate-subtropical coastal rainforests through capacity to endure dry, cool conditions. This southern flora, with more evergreen, thicker, and smaller leaves than the Arcto-Tertiary Flora to the north, soon spread in Oligocene and Miocene time over much of the drier Southwest (Axelrod, 1950a, 1950e, 1958, 1973, 1979).

Most exotic to Californians would be the subtropical thornscrub, retained now only in part in the microphyllous woodland and mixed desert-scrub of the warmer Colorado Desert. It contained many trees and shrubs with small leaves or leaflets, and often with spines, of such genera as *Acacia*, *Bursera*, *Castela*, *Celtis*, *Cercidium*,



*Colubrina*, *Condalia*, *Crossosoma*, *Dodonaea*, *Euphorbia*, *Eysenhardtia*, *Fouquieria*, *Jatropha*, *Karwinskia*, *Leucaena*, *Lycium*, *Lysiloma*, *Mahonia*, *Olneya*, *Pachycormus*, *Piscidia*, *Pithecellobium*, *Prosopis*, *Prunus*, *Psoralea*, *Randia*, *Thouinia*, *Xanthoxylum*, and *Ziziphus*, the palms *Brahea*, *Sabal*, and *Washingtonia*, the arborescent *Nolina*, the vines *Cardiospermum* and *Passiflora*, and such larger leaved genera of trees as *Diospyros*, *Ficus*, *Quercus*, and *Trichilia* as found in the Anaverde, Mint Canyon, Mount Eden, and Tehachapi floras (Axelrod, 1937, 1950a, 1950b, 1950c, 1973). Although it required adequate summer rainfall and mild winters, the thornscrub occupied semiarid slopes. This vegetation today is best developed south of the border where rain falls mostly in the warm season and frosts are rare or absent (*Trichilia* species, for example, require such freedom from frost).

#### LATE MIOCENE-PLIOCENE-EARLY PLEISTOCENE

The Baja California peninsula is believed to have begun its separation from continental Mexico in Middle Miocene time, but with most of the rifting and spreading taking place in the last 6–4 Ma, with movement northwestward of perhaps 260 km (Larson et al., 1968; Seyfert & Sirkin, 1979). What is now southern California west of the San Andreas Fault likewise moved northwestward in Early Pliocene about 300 km in the last five Ma (Atwood, 1970). Right-slip movements offshore have apparently displaced the California islands 120–160 km also northwestward (Axelrod, 1979).

Precipitation decreased in late Miocene with apparent elimination of the short-tree forest from the present desert areas of southern California and impoverishment of the oak-conifer woodland and thornscrub, as indicated by the Ricardo and Anaverde floras from the western Mojave (Axelrod, 1939, 1950c, 1979). Because aridity peaked about 5–8 Ma, it is likely too that semidesert patches increased in number and extent in drier areas of southern California toward the close of the Miocene.

Previous to Pliocene time the sclerophyllous woodland that blanketed the present deserts of southern California, along with a similar flora over most of the area, spoke for a single Mojavean phytogeographic province over what are now the Mojave and Colorado deserts. With the elevation of the Mojave area during the Pliocene,

the resulting colder climate eliminated most of the thornscrub and other more tropical elements from the Mojave highlands and replaced them largely with Great Basin taxa from the north. The lower, warmer Colorado Desert to the south formed then a distinct Coloradoan phytogeographic unit with many thornscrub and other subtropical taxa and a great diversity of life forms. For the most arid sites of the Colorado Desert a semidesert flora can be inferred (Axelrod, 1979).

In late Pliocene-Pleistocene time the elevation of the Sierran, Transverse, and Peninsular ranges, as discussed above, created the regional rain-shadow deserts of southern California. At the same time the increasingly colder California Current off the southern California coast restricted the summer rains farther south. Those floristic elements requiring summer precipitation and warmer winter temperatures were eliminated from the California deserts and found refuge in more southern divisions of the Sonoran Desert. From the various plant formations that had vegetated the present desert or adjacent areas those Madro-Tertiary species preadapted to arid desert conditions presumably moved directly or via arid pockets of semidesert vegetation into the open ecological niches to form the basis of our present desert flora during the Pleistocene interglacials and subsequent Holocene time. Some of the movements of the local vegetation during the last, Wisconsin, glacial episode and the postglacial period are discussed below.

#### PRESENT DESERT VEGETATION

If our California deserts are largely of Late Pliocene-Pleistocene age, the desert plant communities are even more recent, having evolved from existing Madro-Tertiary plant formations as the desert-forming rain-shadows developed. These plant communities are of Holocene age, i.e., they acquired their present distribution and composition during the last 8,000–11,000 years since the retreat of the last, Wisconsin, episode of the numerous cycles, perhaps 19 or 20 according to Imbrie and Imbrie, (1979), of Pleistocene continental glaciation. The Wisconsin peaked from 21,000–11,000 years ago (as interpreted by Cole, 1982).

We have been treated to a relatively clear concept of the vegetation of the Great Basin, Mojave Desert, Colorado and other subdivisions of the Sonoran Desert since Wisconsin time through the efforts of many botanists and paleontologists.



Laudermilk and Munz (1938), Martin, Sabels, and Shutler (1961), and Martin and Sharrock (1964) have studied the coprolites of ground sloths, carnivores, and man. Martin (1964), Martin and Gray (1962), Martin and Mehringer (1965), Mehringer (1965, 1966), and Mehringer and Haynes (1965) have used pollen analysis to interpret Pleistocene and Holocene desert environments. Especially productive has been the study of packrat (*Neotoma*) middens by Wells and Jorgensen (1964), Wells and Berger (1967), Mehringer and Ferguson (1961), Van Devender and King (1971), Lanner and Van Devender 1974, Phillips and Van Devender (1974), King (1976), Van Devender (1976), Van Devender and Mead (1976), Wells (1976, 1983), Wells and Hunziker (1976), Van Devender and Spaulding (1979), Cole (1982), Wells and Woodcock (1985), Cole and Webb (1985), and Cole (1986). Dendrochronology has also been useful.

Apparently until early Holocene time (ca. 9,000 years ago), the Mojave Desert lowlands were vegetated by a coniferous woodland of low-statured junipers and pinyons, chiefly *Juniperus osteosperma* (Torrey) Little and *Pinus monophylla* Torrey & Frem., or solely of juniper, accompanied by *Yucca brevifolia* Engelm. in S. Watson, *Yucca whipplei* Torrey, *Coleogyne ramosissima* Torrey, and *Artemisia*, *Ephedra*, and *Opuntia* spp., and other xerophytes (Wells & Berger, 1967; King, 1976; Wells, 1983; Wells & Woodcock, 1985). Absent from these woodlands were such hot desert plants as *Larrea divaricata* Cav. and *Ambrosia dumosa* (A. Gray) Payne. The first *Neotoma* records of *Larrea* in the Mojave Desert are from the north side of the Ord Mountains about 7,400 years ago (Wells 1983) and from the Lucerne Valley side of the same range to the south at about 5,800 years ago (King, 1976). Vasek (1980) has estimated the oldest *Larrea* clones in the nearby Johnson Valley at about 7,800 years. Presumably the hot-desert species like *Larrea* found refuge during the glacials in the low, warm Colorado Desert (Wells & Berger, 1967). *Larrea* has been reported in Death Valley (Wells & Woodcock, 1985) no earlier than 1,990 + 160 years ago.

In a study of *Neotoma* middens in the very arid lower Colorado River Valley about Picacho Peak, Imperial County, California, at elevations of 245–300 m, Cole (1986) documented 12,500 years to the present of creosotebush desert scrub dominated by *Larrea divaricata*, *Encelia farinosa* A. Gray ex Torrey, and *Peucephyllum*

*schottii* (A. Gray) A. Gray. He considered this hyperarid area to be a Pleistocene desert refugium. At this site Joshua tree, *Yucca brevifolia*, perhaps the most characteristic Mojave Desert species and now largely restricted to the Mojave, was present about 12,500 years ago, and associates, such as *Brickellia arguta* Robinson, *Chrysothamnus teretifolius* (Dur. & Hilg.) Hall, *Coleogyne ramosissima*, *Lycium cooperi* A. Gray, *Salvia mohavensis* Greene, and *Yucca whipplei* Torrey, none now known in the immediate area, were present into the early Holocene until nearly 10,000 years ago. The authors also mentioned late Wisconsin and early Holocene *Pinus monophylla* from as low as 460 m in the Tinajas Altas Mountains of Arizona and a more xeric juniper (probably *Juniperus californica* Carr.) woodland from 600 to 240 m in the Whipple, Chemihuevi, Tinajas Altas, and Butler mountains [until about 8,900 years ago, according to Van Devender (pers. comm.)].

In contrast, *Ambrosia dumosa*, *Fouquieria splendens* Engelm., and *Olneya tesota* A. Gray appeared in middens only less than 600 years old. Possibly these and other Sonoran, hot-desert plants requiring warm temperatures and summer rainfall, had found refuge farther south in the Arizona and Mexican portions of the Sonoran Desert, returning for short periods in each interglacial.

The Mojave Desert in turn served as a refuge for the cold-desert plants, as well as the pinyon-juniper woodlands, which in Holocene time returned to the Great Basin to become the dominant vegetation there. *Pinus flexilis* James and *P. longaeva* Engelm., now absent from Mojave Desert ranges, were recorded by *Neotoma* from the Clark Mountains about 20,000 years ago, with *P. longaeva* already absent and *P. flexilis* rare by 12,460 BP (Mehringer & Ferguson, 1969). Wells and Woodcock (1985) reported *Yucca whipplei* in Death Valley as early as 19,550 + 650 BP along with *Atriplex confertifolia* (Torrey & Frem.) S. Watson and *Opuntia basilaris*, and somewhat later (about 17,000 to 9,500 BP) *Chrysothamnus teretifolius*, *Purshia glandulosa* Curran, and *Haplopappus cuneatus* A. Gray. *Ambrosia dumosa* appeared there by 10,230 + 320 BP, but *Larrea* not until 1,990 BP.

The presence of large, grazing mammals, such as horses, camels, bison, and mammoth, and such browsers as mastodons and ground sloths in the Mojave Desert during the Pleistocene pluvial periods would seem to require that the coniferous



woodlands probably were well supplied with grasses and other edible herbage. The China Lake faunule included two species of camels, two horses, a bison, a mammoth, a deer, and such carnivores as the saber-toothed cat (*Smilodon*), a dire wolf, and a coyote (Fortsch, 1978). Fortsch designated it a Rancholabrean fauna, and cited one preliminary age determination of fossil ivory from a mammoth at 18,600 + 4,500 years BP. Davis and Panlaqui (1978) inferred from this faunule that Lake China could be reconstructed as a "shallow, wind-stirred, fresh water lake; marshes, sloughs and sluggish streams surrounding the lake; some gallery forests of lakeside trees. These aquatic habitats were surrounded, at times, by a tall-grass savanna . . . . However, during the heights of the stadials, the environmental background of Lake China was evidently a cold steppe with some xeric, desert forest such as juniper." The PaleoIndians, who were general foragers, preyed occasionally upon the large herbivores, and were considered by Davis and Panlaqui to be culturally and linguistically complex by 15,000 BP.

Another site of Late Wisconsin/Holocene Transition time, in which early American man is known to have overlapped with now extinct large herbivores, is the Lehner Mammoth site in southeastern Arizona, from which the fossil pollen was studied by Mehringer and Haynes (1965). Clovis fluted points, butchering tools, and charcoal were found there associated with the remains of mammoth, horse, tapir, and bison. Both grazing mammals and the pollen gave evidence of desert-grassland 11,200 years ago.

Packrat midden studies in Death Valley established a 1,200–1,500 m downward displacement of juniper woodland 13,000–19,000 years ago (Wells & Woodcock, 1985). Similar studies in the Grand Canyon have suggested up to a 1,000 m climatic depression during the full-glacial period (21,000–15,000 years ago) of most plant species, particularly in the juniper and blackbush scrub communities (Phillips & Van Devender, 1974; Cole, 1982). These findings support, at least for higher-elevation deserts, a model of latitudinal displacement of climate. King (1976) concluded that his packrat midden data from the Lucerne Valley of the Mojave Desert suggested a 365 m depression of *Juniperus osteosperma* woodland between 12,100 and 7,800 years ago. In a study of Neoglacial vegetation changes in Greenwater Valley near Death Valley, Cole and Webb (1984) found a downward shift

of 50 to 100 m in plant communities during the past 500 years. Thus, the latitudinal and elevational movement of plant communities is still going on, along with the addition to and deletion of species from the communities. Our present desert plant communities are not only very recent, they are highly dynamic, indeed kaleidoscopic in content and location.

#### ORIGINS OF THE CALIFORNIA DESERT FLORA

The present California desert flora is largely composed of autochthonous elements from the Madro-Tertiary Geoflora that dominated southern California and adjacent areas throughout the Tertiary. Other, rarer floristic elements, also preadapted to long periods of drought, hot, dry summers, and cool, wet winters, have arrived from other parts of America and the rest of the world to complete the desert flora. These latter elements deserve some discussion.

In addition to the rather obvious Sonoran elements, Mexico has supplied many of the allochthonous floristic elements found in the California deserts. From their distribution and that of their closest relatives, it would appear that *Mortonia utahensis* (Cov.) Nelson (Prigge 1983), *Buddleja utahensis* Cov., *Yucca brevifolia*, *Y. schidigera* Roezl ex Ortgies, *Yucca whippleyi*, *Castela emoryi* (A. Gray) Moran & Felger, and *Pilostyles thurberi* A. Gray, among others, have arrived in California from the southeast, probably from the Chihuahuan Desert of northern Mexico. *Fouquieria splendens* Engelm., now very conspicuous in the Colorado and other subdivisions of the Sonoran Desert along with several of its congeners in Baja California, has most of its relatives in mainland Mexico, south to Oaxaca (Henrickson, 1972). Other possibly non-Sonoran Mexican immigrants are such plants as *Selinocarpus nevadensis* (Standley) Fowler & Turner, *Pholisma arenarium* Nutt. ex Hook., *P. (Ammobroma) sonorae* (Torrey ex A. Gray) Yatskievych, and *Proboscidea althaeifolia* (Benth.) Duchesne, all with strong relationships to the south with Mexican, but with no close Californian, relatives.

South America has surely supplied a number of California desert plants, not the least being the creosote-bush, *Larrea divaricata* Cav. [or *L. tridentata* (Sessé & Mociño ex DC.) Cov. for those who consider it a distinct species], surely the most widely distributed, abundant, and often dominant woody plant in the warm deserts of North America. The North American desert plant, so



closely similar to an Argentine species both morphologically and biochemically as to be probably conspecific with it, has differentiated cytogeographically since its arrival in North America (Wells & Hunziker, 1977). The Chihuahuan Desert race retains the ancestral diploid condition but the Sonoran and Mojave Deserts have derived tetraploid and hexaploid races respectively. The recent advent of *Larrea* in the Mojave Desert has been discussed above. Although *L. divaricata* has races in South America as far north as Peru, the North American races have closer biochemical affinity with the Argentine race. *Larrea* probably was carried to Mexico directly from Argentina or Chile by migrating birds, and subsequently moved from the Mexican deserts into the Californian deserts in late interglacial and Holocene time.

Other distinctive woody species with probable South American ancestry are *Frankenia salina* (Molina) I. M. Johnston, disjunct between western Mexico-California and Chile, the capparaceous *Koeberlinia spinosa* Zucc., disjunct between the North American Southwest and Bolivia, and *Atamisquea emarginata* Miers, disjunct between northwestern Mexico-Arizona and Argentina-Chile. The North American desert species of the oleaceous *Menodora*, mimosoid *Prosopis* and *Prosopidastrum*, and solanaceous *Lycium* and *Nicotiana* likewise have strong links with temperate South America. *Menodora* and *Lycium* have representatives as well in southern Africa, and *Nicotiana* also in Africa, Australia, and Polynesia. *Thamnosia* of the Rutaceae seems to be unrepresented in South America but does have species in southwestern Africa, the Horn of Africa, and Arabia. Possibly it followed migratory routes somewhat similar to those of *Menodora*, *Lycium*, and *Nicotiana* with subsequent loss of representation in temperate South America. In contrast, *Selinocarpus* of the Nyctaginaceae, mostly of the North American Southwest, has a species in Somalia, like *Thamnosma*, but no species in southern Africa or South America. Most of the desert herbaceous genera that have links to South America appear to have evolved in North America and to have been carried south to temperate South America relatively recently, no doubt also by migratory birds (Raven, 1963; Thorne, 1973).

The more northern elements of the California deserts have apparently entered the warmer deserts from the Great Basin Semidesert. The linkage of many of these genera seems to be strong

with the arid areas of central Asia. Among the more prominent desert genera with a possible Asian origin are *Artemisia*, *Atriplex*, *Ceratoides* (*Eurotia*), *Kochia*, *Mahonia*, *Monolepis*, *Prunus* subg. *Amygdalus*, *Stipa*, and *Suaeda*. These could have reached the New World via Beringia, probably at different times. Some, like *Artemisia*, have speciated rather heavily in western North America, suggesting that they may have been early immigrants.

The linkage between the Mediterranean region with members of both the Californian and Transmontane botanical regions also seems surprisingly strong considering the distant disjunction involved. Porter (1974) believed that the North American taxa of the zygophyllaceous *Fagonia* may be derived from North African species and that the South American species may have independently reached there from South Africa. Likewise, *Peganum mexicanum* A. Gray, indigenous to the Chihuahuan Desert, may be derived from a North African ancestor although the genus reaches also to central Asia and Mongolia. *Oligomeris linifolia* (Vahl) Macbr., ranging from eastern Mexico across Texas to our southwestern deserts, also occurs in the Mediterranean region. It is the only species of the Resedaceae apparently indigenous in the New World. *Plantago ovata* Forsskal (*P. insularis* Eastw.) and *Senecio flavus* (Decne.) Schultz-Bip. (*S. mohavensis* A. Gray) have a similar distribution. Some of these species may be recent immigrants, having entered with the early Spanish conquistadors. Other southwestern desert genera with strong relationships to the Mediterranean region are *Antirrhinum*, *Cupressus*, *Juniperus*, *Pistachia*, and possibly *Astragalus*, *Lupinus*, and *Trifolium*. Some of the Arcto-Tertiary elements, like *Acer glabrum* Torr., *Amelanchier utahensis* Koehne, *Fraxinus anomala* Torr. ex S. Wats., *Philadelphus microphyllus* A. Gray, and *Ribes* spp., that have found refuge in the more mesic highlands of the Mojave Desert have more ancient linkage with eastern American and Eurasian representatives.

Thus the flora of the California deserts is of most diverse origin, having been assembled from both adjacent and far-distant sources. Many elements have reached the Southwest by relatively normal overland movement of propagules over long periods of time, propelled no doubt by changing climate. Others may have crossed narrowed straits, seas, or even oceans when sea-level was lowered in glacial epochs, or much earlier



when continents were closer to one another, although later to be forced widely apart by sea-floor spreading and other plate-tectonic movements (Thorne, 1978). Changes in oceanic-current patterns surely were sometimes involved. In other instances, as especially in the amphi-tropical American disjunctions, the only logical explanation has to be long-distance carriage by migratory birds.

This assembling of the Southwestern desert flora has been going on for tens of millions of years, certainly from late Cretaceous to Holocene time. Some of the most distinctive desert taxa, mostly with no close living relatives, could have evolved in Early Tertiary or even Late Cretaceous time. Among them can be listed such endemic western American taxa as the Crossosomataceae, Fouquieriaceae, Garryaceae, Krameriaceae, Lennoaceae, and Simmondsiaceae. It is likely that some of the herbaceous genera that have speciated so heavily in the southwestern deserts to produce the abundant ephemeral annuals have done so in the Holocene, some possibly in the past couple thousand years. Among them are *Astragalus*, *Camissonia*, *Chamaesyce*, *Chorizanthe*, *Cryptantha*, *Descurainia*, *Eriogonum*, *Gilia*, *Lupinus*, *Mimulus*, *Nemacladus*, and *Phacelia*.

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